XXIX.—*The Origin of the Vertebrates.*

By Edmond Perrier *.

Since the researches of Kowalevsky (1866) the Vertebrates have been successively derived by authors from indeterminate animals (Scolecida), which were considered to have given rise at the same time to the Tunicates (Hæckel, 1866); from the Annelid Worms (Semper, Balfour, 1874; Dohrn, 1875; E. Perrier, 1881; Leydwick Minot, 1897); from the primary Merostomata (Albert Gaudry, 1883); from *Balanoglossus* (Bateson, 1884); from the Nemertines (Hubrecht, 1887); from the Arachnids (Patten, 1891); from the Crustaceans (Gaskell, 1891); from an animal allied to the Appendicularidæ (Brooks, 1893; Willey, 1894).

Differences of opinion such as these evidently imply either that the principles of zoology are still badly defined, or else that they are too frequently lost sight of, or else again that sufficient attention has not been paid to determining the nature of the characters of Vertebrates, the explanation of which had to be demanded from ancestral forms. We hope to show in the present paper that a rigorous application of undisputed principles leads to a unique solution of the problem, and that this solution is in every respect satisfactory.

The following essential characters are exhibited by every Vertebrate:—

(1) The body is bilaterally symmetrical and metamerically segmented throughout its entire length; (2) an important extent of its external or internal surfaces, especially those devoted to the respiratory function, is clothed with vibratile cilia; (3) during the embryonic period, at the very least, the anterior region of the alimentary canal always communicates with the exterior by means of lateral clefts; (4) the circulatory apparatus is closed, and exhibits a heart situated below the alimentary canal; (5) the secretory apparatus is constituted by a system of ducts which are repeated, in the embryo, throughout the whole length of the body, and provide the genital apparatus with its excretory ducts; (6) above the digestive tract there extends, in the embryo, a solid cord of cells, the *notochord*, around which are formed the vertebræ of the adult animal; (7) above the notochord lies the central nervous system, all on the same side of the alimentary canal, deprived of an œsophageal ring, and exhibiting a considerable bulk; (8) with

* Translated by E. E. Austen from the 'Comptes Rendus,' t. cxxvi. no. 21 (May 23, 1898), pp. 1479–1486.

reference to the outer world, the heart and the longitudinal nervous axis occupy contrary positions in the Vertebrates and the segmented Invertebrates, so that if we apply the term *ventral* to the side of the body turned towards the ground, and call the opposite side *dorsal*, the nervous axis is dorsal in the Vertebrates and ventral in the segmented animals, and the contractile vessels are situated on the side of the body opposite to the nervous system.

These are the only characters common to all Vertebrates, including *Amphioxus*; and since no one disputes that all these animals can easily be derived from the simplest forms among them, once these eight groups of characters are explained it must be admitted that the theory of the Vertebrate is complete; conversely, every system of genealogy which should fail to explain these eight groups of characters must be rejected.

(1) *Metamerism of the Vertebrate Body.*—Whatever be the cause of metamerism—a cause that we shall examine in a subsequent communication—the formation of the segments in all the metamerically segmented animals is a precocious developmental phenomenon, the mechanism even by which the body is constituted; by this process many organisms are formed the segments of which may afterwards become obliterated, but an organism not formed by this process once constituted never divides again into well-defined segments. The law of patrogony (repetition of the genealogy by the embryogeny)—a fundamental law universally accepted—is therefore opposed to the possibility of attributing to the Vertebrates an ancestor whose body was not clearly segmented in the adult state, or at the very least multisegmental during the embryonic period. This at once excludes the Nemertines, *Balanoglossus*, and the Appendicularidæ, and leaves only the Arthropods and the Annelid Worms. In truth, in the embryos of these animals the septa between the segments are complete, while in those of the Vertebrates they are confined to the dorsal half of the body; but the embryogeny of *Amphioxus* shows that this is a result of *tachygenesis* or *embryogenic acceleration*. The segmentation of the embryos of *Amphioxus* is at first complete (Hatschek), and consequently identical with that of the Annelid Worms; afterwards the ventral portion of the septa is absorbed again; this condition is realized at once in the Vertebrates proper.

(2) *The Vibratile Cilia.*—The entire organization of Arthropods is to some extent dominated by the property which their epithelial elements possess of forming, in their superficial region, a deposit of chitin, which causes this region

to mortify, and renders it unsuited to the development of vibratile cilia. This property manifests itself in these animals almost at the very beginning of the development of the embryo (*Nauplius*); it has rendered necessary the ecdyses which have in their turn occasioned the metamorphoses; the absence of the cilia has had to be compensated for by the formation of jointed legs, moved by striped muscles and having the respiratory apparatus dependent upon them. Commencing at any rate from the precocious period which the *Nauplius* represents in their ontogeny, the evolution of the Arthropods has therefore taken quite a peculiar direction, and they have remained isolated from all animals the epithelia of which have continued to be wholly or partially ciliated. If the law of patrogony is correct, which no one disputes, there cannot exist beyond the Rotifers (SCIRTOPODA) a transitional form between them and the long uninterrupted series of the Nephridiates which proceeds from the Rotifers to the Vertebrates inclusively. This excludes them from the lineage of the Vertebrates, the apparent resemblances between which and the Merostomata, the Arachnids, or the Crustaceans are only cases of convergence. In particular the protective shields of the placoid fishes are actual bones formed in the derm, and not a simple epidermic covering like the pieces of the Arthropod carapace.

(3) *Branchial Clefts.*—The presence of lateral branchial clefts in *Balanoglossus* and in the Appendicularidæ has been one of the great arguments that have been invoked in favour of their relationship with the Vertebrates. This relationship is undeniable in the case of the Appendicularidæ, but the absence of embryonic segmentation in these animals proves (law of patrogony), as we have already pointed out, that they are not ancestral Vertebroids, but degraded Vertebroids; the same remark would apply to *Balanoglossus*, in case we were to admit as real the resemblances which people have *striven* to find between it and the Vertebrates, apart from its branchial clefts. But this latter resemblance is itself open to suspicion. The branchial clefts of the Vertebrates and the primary and secondary branchial clefts of *Amphioxus* are repeated, in fact, exactly like the metameres; although the embryo of *Balanoglossus* exhibits manifest traces of metameric segmentation, there is no relation between the metameres and the branchial clefts. This would be explained, for once in a way, as is shown by the discord which finally supervenes in the case of *Amphioxus* itself, under the supposition of a degeneration on the part of *Balanoglossus*, but not on the hypothesis which makes it an ancestral form. The absence of branchial clefts

in the Annelid Worms is an objection that may be lodged against the annelidan theory of the Vertebrates. It is easily disposed of. The branchial clefts are, in fact, but adventitious orifices of lateral diverticula of the alimentary canals. Now many Annelid Worms exhibit such diverticula; they are also produced in the Turbellaria and the Nudibranch Mollusks, which are nephridiates, and in this case these diverticula may open to the exterior (*Yungia*, *Cycloporus*, ÆOLIDIDÆ).

Balanoglossus itself, were it the ancestor of the Vertebrates, would come to be intercalated between them and the Annelid Worms, and would bear witness to the possibility of the appearance of pharyngeal clefts in these latter. The phenomena of budding in various CTENODRILIDÆ, SYLLIDÆ, and SERPULINÆ, as well as in the NAIDOMORPHA, also demonstrate the possibility of the appearance of adventitious orifices to the digestive canal in the case of the Annelid Worms properly so-called.

(4) *Circulatory Apparatus.*—Among the ancestors attributed to the Vertebrates, the Annelid Worms, the Nemertines, and *Balanoglossus* have, like the Vertebrates themselves, a closed circulatory apparatus; on the other hand, no Arthropod is known the circulatory apparatus of which is not in part lacunar. On this head the Arthropods are therefore excluded for the second time. The circulatory apparatus of the Nemertines has no differentiated propulsive centre; that which is called the *heart* in *Balanoglossus* is an organ situated on the same side of the alimentary canal as the nervous axis, and cannot consequently be homologous with the heart of the Vertebrates; the Annelid Worms therefore alone exhibit the typical relations of the circulatory centres, alimentary canal, and nervous axis, which are observed in the case of the Vertebrates.

(5) *Nephridial Apparatus.*—The urinary apparatus of the true Arthropods * is constructed after quite a different type from that of the nephridial apparatus of the Annelid Worms, the Nemertines, *Amphioxus*, and the Vertebrates; this apparatus appears to be wanting in *Balanoglossus*, which thus furnishes a new motive for its exclusion; in the case of the Annelid Worms and in *Amphioxus* it is formed of independent ciliated tubes, opening into the general cavity on the one side and to the exterior on the other, and recurring regularly either in almost all the segments of the body or only in a certain

* Among these *Peripatus* cannot be included with certainty, in spite of the attempts that have recently been made to connect it with them.

number of them, the anterior segments, for instance (Amphictenidæ, Ampharetidæ, Terebellidæ, *Amphioxus*). The nephridia of the Nemertines are also confined to the anterior region of the body, and eventually open into a collecting duct on each side; herein they seem to present a further resemblance to those of the Vertebrates: but analogous conditions exist in the case of the Annelid Worms (*Loimia medusa*, *Lanice conchylega*); in certain Lumbricidæ (*Octochætus*, *Perichæta*) and some Hirudineans (*Pontobdella*) the nephridia form throughout the body but one and the same system of reticulated tubes. Moreover, in the Annelid Worms the nephridia almost always place themselves more or less at the service of the genital apparatus, as in the case of the Vertebrates. In the Earthworms (Lumbricimorpha) there even occurs a doubling of the renal apparatus and of the excretory apparatus of the genital glands, the analogies between which and that which is observed in the case of the Vertebrates (Wolffian and Müllerian ducts) I set forth as early as 1881 *. The advantage therefore rests with the Annelid Worms, of which the Nemertines are in all probability nothing but highly modified forms. The Annelid Worms being henceforth alone concerned, it remains for us to explain how it has been possible for them to be the point of departure for the organic conditions which are peculiar to the Vertebrates.

(6) *Notochord.*—If it has been possible to compare for one moment the endodermic diverticulum of the proboscis of *Balanoglossus*, or even the proboscis of the Nemertines with the *notochord* of the embryos of Vertebrates and of the Tunicates, it is in default of having rigorously defined the conditions which have brought about the formation of the notochord and the necessary relations which result from this formation. The embryogeny of *Amphioxus*, like that of the Tunicates, shows in fact that the notochord is originally not a cord of cells, but the entire region of the endoderm included between the rudiment of the nervous system and the two rudiments of the mesoderm. These three rudiments are three regions of active development, which are only able to derive the reserve of nutriment which is necessary for them from the endodermic area comprised between them. As a result of this the elements belonging to the area thus circumscribed empty themselves, become vacuolate and to a certain extent mortified; the rest of the endoderm, on the contrary, continues to develop, glides in consequence underneath the inert area and eliminates it from the endoderm, and it is this

* 'Les Colonies animales,' pp. 677 and 684.

eliminated area, the origin of which is quite clear, which, by the grouping of its elements into a cord, constitutes the notochord The cord thus constituted has nothing except the mortification of its cells in common with the endodermic diverticulum which penetrates into the proboscis of *Balanoglossus* and which has its analogue in the case of *Cephalodiscus*. These structures can be no more likened to a notochordal rudiment than could the median diverticulum, entirely analogous this time to that in *Balanoglossus*, which is thrown out in front by the main intestine of the majority of the polyclad and triclad Turbellarians. On the contrary, it will easily be understood how it has been possible for a notochord to be formed in an Annelid Worm, of which the nervous system, developed to an exceptional degree, and the mesodermic rudiments have been affected by tachygenesis. Now the formation of the nervous system by an invagination of the ectoderm and that of the mesoderm by two evaginations of the endoderm are evident proofs of the intervention of tachygenesis *. The considerable proportions assumed by the nervous system furnish, moreover, the explanation of the two latter distinctive characteristics of the Vertebrates.

(7) *Disappearance of the Œsophageal Ring.*—The exceptional volume assumed by the nervous system in all Vertebrates excludes from their genealogy *Balanoglossus*, in which, on the contrary, the axial cord is reduced to a very short rudiment which does not exceed the collar in length. The proportions to which the nervous axis attains necessarily induce its precocious development, its formation by rapid processes. It originates, in fact, at the expense of a fairly large area of the ectoderm, which buries itself beneath the neighbouring regions at a period well in advance of that at which the mouth is constituted. The nervous system being outlined before the mouth has no longer to concern itself with the existence of the latter, as it does in the case of the Annelid Worms, by developing around it. There is no longer a *raison d'être* for the œsophageal ring †; it disappears, and the brain proceeding to its completion on the median neural line stands in the way of the formation of the mouth upon this line. It is the cause of the reversal of the attitude of the Vertebrates, as already pointed out by Geoffroy Saint-Hilaire.

(8) *Reversal of Attitude in the Vertebrate.*—The mere comparison of a section of the embryo of a dog-fish and of a

* See 'Comptes Rendus,' December 1896: Report on the Competition for the Serres Prize, by the author.

† E. Perrier, 'Les Colonies animales,' p. 695 (1881).

section of an Annelid Worm suffices to demonstrate, as was proved by Semper, after Geoffroy Saint-Hilaire, that the inverse arrangement of the organs in the two branches is easily explained by a simple change of attitude. If we consider the embryogeny of *Amphioxus*, such as it has been described by Hatschek and, most recently, by Willey, keeping before us the considerations of which a *résumé* has been given above, all the apparently inexplicable peculiarities in the development of this animal not only become cleared up of themselves, but show the way in which the inversion of the higher Vertebrates has come to pass. The mouth of *Amphioxus* does not pass indeed all at once to the median line, opposite to the line of the nervous axis; it is formed at the nearest possible point to its primitive situation, on the left side of the body. The mouth having become lateral, the animal cannot feed except on condition that it lies on the left side of the body, which becomes its habitual attitude. According to Lamarck's principle (*use and disuse of organs*), of which the entire history of the Invertebrates is also a striking confirmation, it results from this new attitude that the organs of sense of the left half of the body, being more in touch with the nutriment supplied by the food, alone develop: the young animal exhibits but one olfactory pit and one gustatory organ (Hatschek's organ), both situated on the left. In consequence of this same attitude all the branchial clefts on the left side are covered up, and it is rendered impossible for them to perform their normal function. The animal is therefore induced to twist the region of its body which corresponds to them, so as to bring all its branchial clefts on to the right side. This is no mere hypothesis; this torsion is exhibited by the young *Amphioxus* in the course of its development (Willey), without any present physiological necessity being able to explain it; its two series of branchial clefts, the projecting folds between which they are enclosed, which are the first traces of the subbranchial cavity of the adult animal, are formed on the right side of the body exclusively and mark out the curves along which the torsion has been accomplished. The application of the law of patrogony necessitates the conclusion that the ancestors of *Amphioxus* passed through a period at which they lived lying on the left side, with the mouth in contact with the ground, and when they were obliged, in order to ensure the regularity of their respiration, to twist the branchial region of the body. This permanent attitude has produced, in consequence of the constant contraction of certain muscles and the relaxation of those opposed to them, an asymmetry of the body which has been transmitted

by heredity (*Lamarck's principle*), and this phase in the history of *Amphioxus* is still found inscribed upon its embryogenic development. Later on the animal adopted the habit of burying its posterior extremity in the sand; it found itself subjected to a life in a homogeneous medium; the symmetrical shapes, acting in harmony with a more ancient heredity unopposed by contrary efforts, and in accordance even with the conformation of the regions of the body which have escaped the torsion, caused the mouth, by means of successive distortions, to take its place in the plan of symmetry, and, since it was unable to regain its position in the dorsal median line, it passed over to the ventral side. Thus was brought about the new attitude and the return to a perfect symmetry on the part of the Vertebrates descending from *Amphioxus* or from analogous Vertebroids *.

XXX.—*Descriptions of new Coleoptera from East Africa.*

By C. O. Waterhouse, F.E.S.

The following interesting new Coleoptera have been lent me for description. They form part of a valuable collection made by Mr. Hollis in Usambara in 1893 and 1894.

* *Amphioxus* in the adult state has not yet recovered this symmetry, as is shown by the presence on the left side of the body of a single olfactory pit, the continuity of the right half of the oral hood with the cephalic expansion of the fin, the continuity of the right metapleure alone with the ventral fin, the overlapping of the right and left muscle-segments, and, finally, the abortion of the genital organs of the left side in *Amphioxus cultellus*, from Torres Straits, and *A. lucayanus*, from the Bahamas, for which have been founded the genera *Epigonichthys* and *Asymmetron*.

The inductions by means of which we have interpreted the phenomena of torsion which are proved to take place in the development of *Amphioxus*, and the deductions which we have drawn from these phenomena with reference to the history of the reversal of the Vertebrates, are but strictly scientific applications of general laws, recognized by all in principle, but too often forgotten in each particular case. We observe, moreover, phenomena of torsion, which are analogous to the above and are explained by the principle of Lamarck, likewise in the development of many fixed animals (Cirrhipedes, Bryozoa, Echinoderms, Tunicates), in the case of the Gastropod mollusks and the Pleuronectid fishes. The rule which governs all these phenomena, and which may be termed the *rule of the fixation of attitudes*, may be expressed thus:—

When, in passing from one mode of life to another, an animal is led, in order to ensure that its organs shall perform their functions properly, to assume habitually a definite attitude, this attitude is capable of becoming fixed and hereditarily transmitted.